

Interrupted Nitrogen Nutrition Effects On Growth, Sucrose Accumulation and Foliar Development of the Sugar Beet Plant¹

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Received for publication October 11, 1962

Under natural conditions, nitrogen supply is frequently limiting to the growth of plants. This may result from seasonal variations in the nitrogen content of soils and in rates of nitrogen absorption and assimilation by plants as well as from a low supply of native nitrogen. In agricultural environments, nitrogen nutrition may be maintained at an optimum level with suitable fertilizer practices. This usually involves more than simply supplying sufficient nitrogen for luxury consumption since the yield and quality of the economically useful yield of many crop species are maximal when nitrogen has been in marginal or deficient supply during critical stages of plant development (8)³. Thus, the response of plants to fluctuations in nitrogen supply is of importance agriculturally as well as biologically.

Sugar beet is well suited to studies on the effects of fluctuating nitrogen nutrition on plant growth. It has an indeterminate vegetative growth habit and tissue analysis procedures (15) have been developed for assessing plant nutrient status. Considerable information has been obtained concerning the responses of sugar beet to nitrogen starvation, (4,5,6,9,11,12) but, except for an experiment by Ulrich (9), much less is known about its recovery from the deficient condition. Such information should have ecological significance as well as having practical application to commercial production.

The experiment reported here was designed to provide information on the time course of the nitrogen starvation and recovery responses of sugar beet. Particular attention was given to changes in leaf growth.

Methods and Materials

Sugar beet plants were grown outdoors in 10-gallon pots at Davis, California, during the 1960 season; environmental data are summarized in Figure 1. Air temperature was recorded at 4.5 feet with a thermocouple and a recording potentiometer. Solar radiation data, obtained with a horizontally exposed Eppley pyrheliometer, were supplied by the Davis weather station.

¹ This study was supported in part by a grant from the beet sugar companies operating in California and the California Beet Growers Association, Ltd.

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³ Numbers in parentheses refer to literature cited.

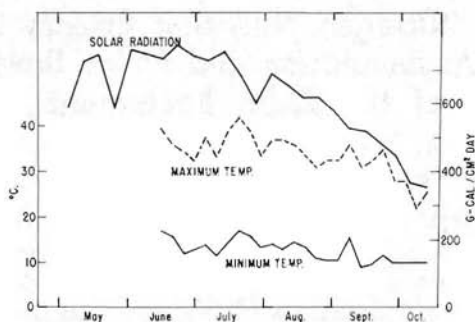


Figure 1.—Maximum and minimum air temperature (5-day means) and solar radiation (7-day means) in the experimental environment.

Cultural procedures were similar to those previously employed (4, 5). The pots (used carbide cans, 32 cm diameter and 52 cm high) were provided with bottom drainage and were filled with no. 2 grade vermiculite. On May 1, 10 seed units (variety MS NB1 \times NB4)⁴ were planted per pot. The seedling plants were thinned at regular intervals, so that by June 10 only two plants remained per pot. The pots were spaced a minimum of 50 cm apart to prevent foliar competition between pots.

An excess of half-strength modified Hoagland's solution made up with tap water (4) was supplied daily to each pot. This level of nutrition was maintained until July 23 when differential treatments were begun. The treatments (Figure 2) consisted of supplying the plants for various lengths of time with a solution free of added nitrogen. The tap water contained 0.04 mmole $\text{NO}_3\text{-N}$ per liter. Experience has shown that the severity of a nitrogen deficiency is not measurably influenced by using solutions ranging from 0.00 to 0.08 mM $\text{NO}_3\text{-N}$ per liter and the low-nitrogen solution used here will be referred to as the minus-nitrogen solution. In this minus-nitrogen solution, CaCl_2 was substituted for $\text{Ca}(\text{NO}_3)_2$ and K_2SO_4 for KNO_3 . The vermiculite was leached with tap water at the start of a nitrogen-deficiency period.

Data on foliar development were collected for key treatments throughout the growing season. Leaf appearance rate was obtained by tagging weekly the smallest leaf over 5 cm in length, and counting the number of leaves between it and the previously tagged leaf. Leaf area per plant was estimated weekly by tracing every fifth living leaf and determining the area with a planimeter. Dead leaves were collected and counted at weekly intervals.

The plants in ten pots from each of various treatments, as indicated in Figure 2, were harvested at three-week intervals

⁴Dr. J. S. McFarlane, ARS, U. S. Department of Agriculture, Salinas, California, provided the seed.

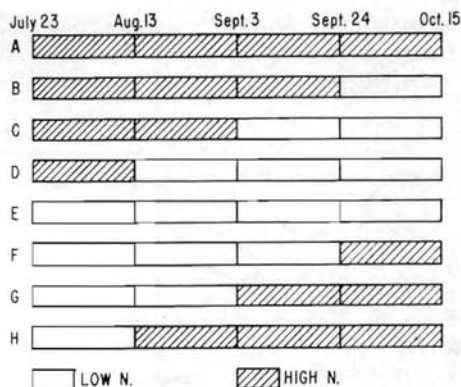


Figure 2.—Treatment combinations. All plants were supplied with high nitrogen until July 23. Minus-nitrogen solution was then used for varying periods of time as indicated. Ten pots of each treatment were harvested at 3-week intervals as follows: July 23—A; August 13 and September 3—A and B; September 24—A, B, C, and G; October 15—all treatments.

beginning July 23. The final harvest on October 15 included 10 pots from every treatment. Eight recently mature leaves were selected from each pot for tissue analysis (3). Roots of harvested plants were separated from tops at the base of the oldest living leaf, washed to remove vermiculite and secondary roots, and the crowns were then cut from the roots at the lowest leaf scar. Fresh weights were recorded for individual roots, tops, and crowns. Dry weight of tops was obtained after drying at 70° C.

The two roots in each pot were pulped together and three 26-gram samples of pulp were frozen on dry ice. These were analyzed later for sucrose (with hot water digestion) by the Sachs-le Docte procedure (2)⁵. One 26-gram sample was taken for dry weight. Sucrose yields were calculated on total beet weight (root + crown) with the assumption that crowns had the same sucrose concentration as roots (4).

Results

Plant nutrient status

Incipient nitrogen-deficiency symptoms usually were apparent within 2 weeks after a group of plants had been changed to the minus-nitrogen solution. After 3 weeks, the older leaves were lighter green and the expanding leaves were smaller than on high-nitrogen plants. Otherwise the general appearance of high- and minus-nitrogen plants was similar. Extended nitrogen deficiency resulted in fewer leaves with short petioles and small, green leaf blades occurring in flattened rosettes. Deficient plants responded

⁵ Sucrose analyses on the frozen samples were made with the assistance of the Spreckels Sugar Company, Woodland, California.

rapidly to nitrogen return with the renewed production of new leaves. Plant tissue analyses (Figure 3) confirmed the rapid development of nitrogen deficiencies and the equally rapid recovery.

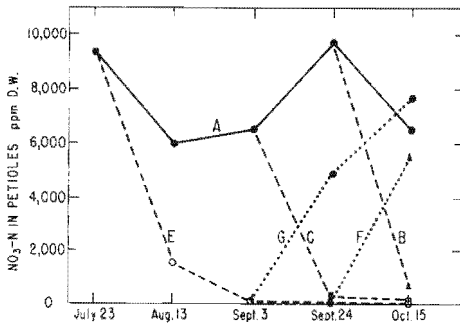


Figure 3.— $\text{NO}_3\text{-N}$ content (ppm dry basis) in petioles of recently mature sugar beet leaves. Critical nutrient concentration is 1000 ppm. Letters refer to treatments.

Growth with high and minus nitrogen

In Figure 4, the nitrogen-deficiency responses shown by treatment E are compared with those of the high-nitrogen control (treatment A). These results are similar to the patterns depicted by Bouillene et al. (1) and Ulrich (10, 11) for high-nitrogen plants and by Ulrich (11) for nitrogen-deficient plants. With high nitrogen, weight of tops and of storage roots increased throughout the 12-week period from July 23 to October 15. On August 13, 3 weeks after nitrogen cut-off, the minus-nitrogen plants could be distinguished from the high-nitrogen plants by appearance, but the weights of tops and of storage roots were equal for the two treatments. Growth rates of tops and of storage roots were sharply reduced by nitrogen deficiency after August 13 and no further increase in root size was observed after September 13. By October 15, high-nitrogen roots were nearly twice as large as those obtained with continuous nitrogen deficiency. The growth of new leaves was reduced and top weight declined as the older leaves died. Size of crowns was greatest with high nitrogen reflecting the greater amount of top growth which had occurred (Table 1).

The sucrose concentration in roots of plants maintained at high nitrogen was relatively constant during the season at about 12% (fresh weight basis). Since this equilibrium concentration has been found to be inversely related to night temperature (10, 12, 14), slightly higher concentrations were anticipated in the fall (Figure 1, Table 2). However, the midsummer sucrose levels

were slightly, but significantly, higher than later values, suggesting that solar radiation (Figure 1) or root size (5) may have been the controlling factor in sucrose concentration.

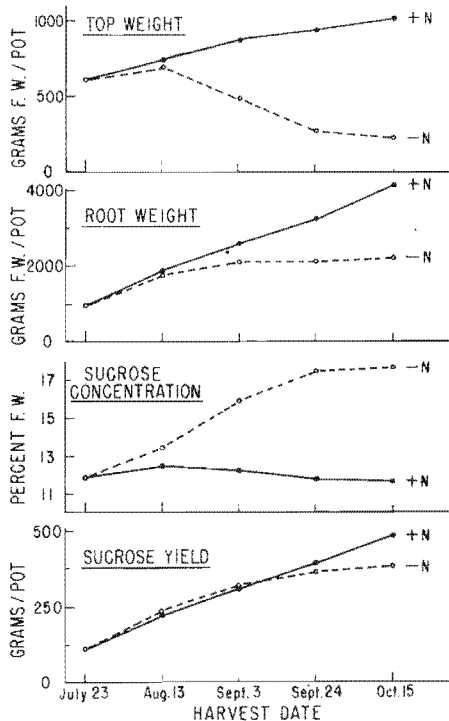


Figure 4.—Time course of sugar beet growth at high (treatment A) and minus nitrogen (treatment E).

Table 1.—Harvest results on October 15 from sugar beet plants grown with varying nitrogen nutrition. (Means of 10 replications).

Treatment	Nitrogen cutoff date	Nitrogen return date	Beet root plus crown				Tops		
			Fresh wt g/pot	Crown %	Sucrose %	Sucrose g/pot	Fresh wt g/pot	Height cm	Diameter cm
A	4100	6.1	11.7	480	1020	30	62
B	9/24	3730	6.3	12.5	468	854	30	60
C	9/3	3460	4.8	13.9	480	582	24	52
D	8/13	2880	4.5	15.7	452	431	19	51
E	7/23	2160	3.2	17.6	379	207	13	48
F	7/23	9/24	2140	3.6	15.7	336	280	18	43
G	7/23	9/3	2550	5.4	13.6	347	407	20	46
H	7/23	8/13	3340	6.9	11.9	396	869	30	59
LSD ₀₅			205	0.9	0.1	28	120	2	3
F ¹			100.4	14.9	188.3	37.0	49.6	67.2	44.9
Error M.S. (72 df)			53.025	1.173	0.2353	964.7	18,176	6.291	10.92
C.V. %			7.6	21.2	3.4	7.4	23.2	10.9	6.1

¹ Required $F_{05} = 2.14$; $F_{01} = 2.90$

Table 2.—Summations of minimum temperatures for 4 weeks prior to various harvest dates and the sucrose concentrations in beet roots observed with high-nitrogen nutrition.

Harvest date	Heat sum ¹ °C-days	Sucrose %
July 23	411	11.9
August 13	412	12.4
September 3	367	12.1
September 24	313	11.8
October 15	296	11.7
LSD ₀₅		0.3
F ₂		6.33 ²
Error M.S. (45 df)		0.12
C.V. %		2.9

¹ Minimum temperatures above 0° summed daily for 28 days prior to harvest.

² Required F₀₅ = 2.58; F₀₁ = 3.77

Nitrogen deficiency caused sucrose concentration to increase gradually at first and then more rapidly; a maximum of 17.4% was reached after 9 weeks of deficiency (Figure 4). Sucrose yields were the same in high- and minus-nitrogen treatments with up to 6 weeks of deficiency indicating that the increase in sucrose concentration compensated for the reduction in root size.

Nitrogen-deficiency treatments (B, C, D) beginning August 13, September 3, and September 24 gave response patterns similar to those shown in Figure 4 for treatment E, but the changes were not as great. As an example, while 17.4% sucrose was attained 9 weeks after the July 23 cutoff, only 15.7% was reached 9 weeks after the August 13 cutoff. On October 15, the high-nitrogen treatment (A), and the 3- and 6-week terminal deficiency treatments (B, C), all yielded similar amounts of sucrose, and while higher sucrose concentrations were obtained after 9 and 12 weeks of deficiency, root weights from these treatments (D, E) were reduced to the extent that less total sugar was produced.

Nitrogen return responses

The influence of a midseason interruption in nitrogen nutrition may be assessed most easily from data obtained on October 15 (Table 1). Root weights were reduced 25% when plants were deficient for 3 weeks (July 23 to August 13; H), even though nitrogen was available throughout the remainder of the growth period. Since this reduction was not apparent on August 13 (Figure 4), it occurred after nitrogen was returned. A 6-week midseason nitrogen deficiency (G) resulted in an even greater reduction in beet root weight. Beet root weight was the same with a 9-week deficiency followed by a 3-week nitrogen return (F) as with 12 weeks continuous deficiency (E). Apparently a brief period of nitrogen return did not effectively stimulate root growth once growth stoppage had occurred.

Sucrose concentrations in the storage roots on October 15 (Table 1) were also influenced by nitrogen return. In general, each 3 weeks of nitrogen-return reduced sucrose concentration approximately 2 percentage units below what would have been attained with continuous minus nitrogen. Thus, 15.9% sucrose was attained by September 3 after 6 weeks of nitrogen deficiency and this was reduced to 13.6% during the subsequent 6 weeks at high nitrogen (G). The increase in sucrose concentration noted after a midseason deficiency of 3 weeks (H) was not retained when nitrogen was returned and this treatment yielded less sucrose per pot than the high-nitrogen control because of the 25% reduction in root weight. At the other extreme, returning nitrogen on September 24 to plants which had been deficient for 9 weeks (F) lowered sucrose concentration but did not increase root weight and this treatment yielded less sucrose than was obtained with continuous nitrogen deficiency (E).

Top development

Number of leaves. The rate of new leaf appearance, as shown for treatments A, E, and G in Figure 5, was markedly affected by nitrogen deficiency. With adequate nitrogen, 4 ± 1 new leaves appeared per plant each week. This rate was maintained throughout the season and was not greatly influenced by changes in plant age or climate. A lower rate of leaf appearance was noted during the second week following induction of nitrogen deficiency; the rate continued to decline to a minimum of < 1 per week by the sixth week of deficiency. Nitrogen-deficient plants maintained this rate for the remainder of the season, apparently by utilizing the small amount of nitrogen in the solution and nitrogen supplied to the apical meristem from other parts of the plant. With later nitrogen deficiency dates (B, C, and D; data not shown), the leaf-appearance rate declined even more rapidly. A greater rate of nitrogen utilization by the larger plants may have accounted for this, as evidenced by tissue analysis date (Figure 3). When nitrogen was returned to deficient plants the rate of leaf appearance increased within 2 weeks to 4 ± 1 per week.

Since the leaf-appearance rate was constant when the plants were supplied with a high level of nitrogen, there was a constant increase in the accumulated total of leaves. By October 15, high-nitrogen plants (A) had produced an average of 74 leaves while plants which had been supplied with minus-nitrogen solution after July 23, produced only 47 leaves. Of particular interest was the observation that no compensatory increase in number of leaves occurred after nitrogen return (G; Figure 5), i.e., the leaf-appearance rate did not exceed 4 per week. A compensatory

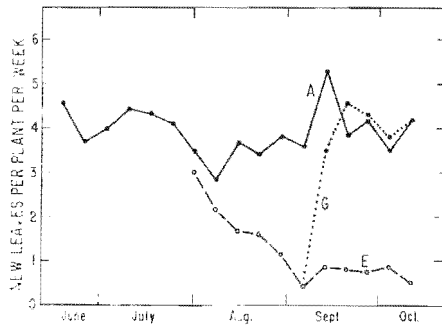


Figure 5.—Number of new leaves per plant which appeared each week with high (A) and minus (E) nitrogen and nitrogen return (G).

increase would be expected if during nitrogen deficiency leaf initiation had continued at the normal rate while leaf expansion and hence leaf-appearance rate were inhibited. Microscopic examination of terminal apices from high- and minus-nitrogen plants failed to reveal any marked differences in the number of leaves less than 5 cm long indicating that leaf appearance and leaf initiation rates were equal.

The number of dead leaves collected was not significantly affected by nitrogen nutrition. There was a tendency for leaves which had matured under adequate nitrogen, to undergo earlier senescence as evidenced by yellowing and to die somewhat sooner when subjected to nitrogen deficiency. However, final counts on October 15 showed equal numbers of dead leaves in both high- and minus-nitrogen treatments. Thus, because of the lower rate of leaf appearance, the nitrogen-deficient plants had only about one half the number of living leaves as the high-nitrogen plants.

Leaf area With high nitrogen, leaf area remained less than 1 dm² per plant during the first month after planting (Figure 6). It increased rapidly thereafter to a maximum of 38 dm² per plant in September and then declined. A decrease in leaf area, which continued throughout the remainder of the season, was apparent after 2 weeks of growth for plants on minus-nitrogen solution. A return to high nitrogen following a 6-week deficiency tended to slow the rate of decline.

The decline in leaf area in late September observed with high nitrogen was due to a smaller size of the new leaves as shown by the leaf growth curves in Figure 7 which are representative of the observations for treatments A, E and G. With high nitrogen (A), the maximum areas of leaves 15-20 were typically about twice those attained by later leaves. In addition, leaves initiated during July and August had slower growth rates than those

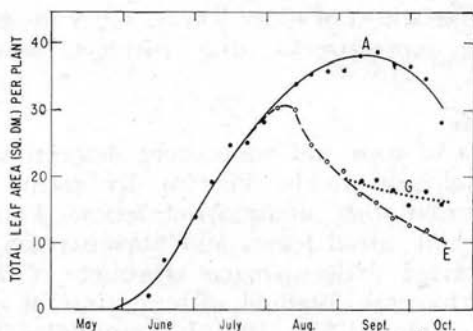


Figure 6.—Total area of living leaves per plant at high (A) and minus (E) nitrogen and with nitrogen return (G).

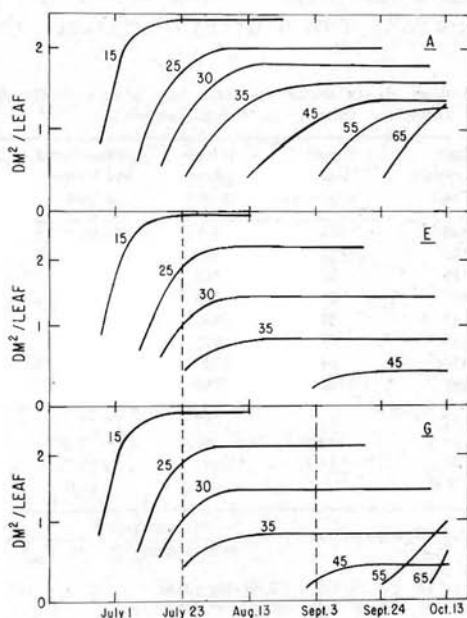


Figure 7.—Stylized growth curves for various leaves at high (A) and minus (E) nitrogen and with nitrogen return (G). These curves are representative of the changes observed for the 20 plants in each treatment.

produced earlier or later. Within 3 weeks after the change to minus-nitrogen solution (E), the enlargement of expanding leaves ceased, and the new leaves which appeared subsequently had small blades and short petioles. When nitrogen was returned to such plants, they continued to produce only small leaves during the subsequent 2 weeks, although the leaf-appearance rate did increase. These new leaves formed a flattened rosette of new

growth within the whorl of older leaves. Only those leaves which appeared 3 or more weeks after nitrogen return enlarged normally.

Biological yields

Dry weights of tops and roots were determined to provide estimates of biological yields. Percent dry matter of both tops and roots increased with nitrogen deficiency. Total dry weight of the whole plant (dead leaves and fibrous roots excluded) at final harvest varied with nitrogen treatment (Table 3). The highest production was obtained with continuous high nitrogen. Production was reduced 5 to 10% by terminal deficiencies of 3 and 6 weeks, although sucrose yields remained unchanged. Thus, the proportion of the total dry weight which occurred as sucrose (coefficient of economic yield; 7) was increased from 48% with high nitrogen to 58% with 6 weeks of nitrogen deficiency prior to October 15.

Table 3.—Distribution of dry matter in sugar beet plants on October 15 as influenced by previous nitrogen nutrition. (Means of 10 replications.)

Treat- ment	Root plus crown g/pot	Green tops g/pot	Whole plant g/pot	Accumulated old leaves g/pot	Season total g/pot	K ¹ %
A	766	143	908	96	1004	48
B	733	125	858	—	—	—
C	727	86	813	93	906	53
D	665	69	734	—	—	—
E	543	37	580	79	659	58
F	496	49	545	—	—	—
G	533	64	597	76	673	52
H	631	122	753	—	—	—
LSD ₀₅	41	11	49	11	51	—
F	49.3 ²	112.3 ²	68.9 ²	7.4 ³	90.3 ³	—
Error M.S.	2140	134.5	2684	137.7	3266	—
C.V. %	7.1	13.3	7.2	13.6	7.0	—

¹ K (Coefficient of economic yield) = $\frac{\text{sucrose yield}}{\text{total season dry wt}} \times 100$; calculated from treatment means.

² Required $F_{05} = 2.14$; $F_{01} = 2.90$. 72 df for error.

³ Required $F_{05} = 2.86$; $F_{01} = 4.38$. 36 df for error.

The net assimilation data (Table 4) indicate that photosynthetic activity was reduced greatly by extended nitrogen deficiency. Net assimilation rates were equal for both high- and minus-nitrogen plants for the first 6 weeks; net assimilation rates for the minus-nitrogen plants then declined to a very low level. Gross assimilation rates cannot be obtained from these data since respiration losses were not estimated. Whole plant respiration was probably less with nitrogen deficiency due to the reductions in growth rate and the smaller size of tops and roots. However, because of the sharp reduction in leaf area, the proportion of the gross photosynthate used in respiration may have increased.

Table 4.—Dry matter accumulation by sugar beet plants at high- and minus-nitrogen status. (Calculations based on means of 10 replications.)

Interval	Continuous high nitrogen (Treatment A)			Continuous minus-nitrogen (Treatment E)		
	Dry wt. increase of tops and roots g/pot	Mean ¹ leaf area dm ² /pot	Mean ² N.A.R. g/dm ² day	Dry wt. increase of tops and roots g/pot	Mean ¹ leaf area dm ² /pot	Mean ² N.A.R. g/dm ² day
7/23 - 8/13	154	58	.126	151	58	.124
8/13 - 9/3	188	70	.128	131	49	.127
9/3 - 9/24	137	74	.088	12	35	.016
9/24 - 10/15	158	68	.111	14	22	.030

¹ Mean leaf area per pot represents the mean of the 4 weekly measurements obtained during the 3-week growth period. See Figure 6 for time course of leaf area changes in treatments A and E.

² N.A.R. (net assimilation rate) defined as grams dry matter accumulated per dm² leaf area per day.

Discussion

The sequence of leaf shapes and sizes observed at high nitrogen is of particular interest. Bouillenne et al. (1) found that "juvenile" sugar beet plants produce a series of leaves with broad, rounded blades and short petioles, while "adult" plants (storage root enlarging) produce leaves with small, narrow blades on longer petioles. Ulrich (13) found that leaf shape is influenced by climate, and that these two shapes are produced in cool and warm climates, respectively. In the present experiment, temperature differences (Figure 1) between early and late summer do not appear to account for differences in the size and shape of leaves; leaves produced during cool weather in September were adult shape, while leaves produced during slightly warmer weather in June were juvenile shape. All leaves were light green with light-colored petioles and thus corresponded to warm climate leaves by Ulrich's criteria (13).

As leaf area per pot increased, transpiration increased and wider fluctuations in water content probably led to internal diurnal water deficits of increasing intensity. While brief wilting was noted only on extremely hot or windy days, moisture variations in the upper half of the available moisture range will influence leaf enlargement (C. B. Shah and R. S. Loomis, unpublished). We have observed that one third of the available moisture in a 10-gallon pot may be used within 24 hours after watering. Thus the tendency towards smaller leaf size and slower leaf growth during August can be attributed in part to moisture deficits. However, this does not explain the continued production of small leaves in September and October when such deficits would have been much less pronounced. It seems likely that physiological age or plant size in some way controlled leaf size.

Nitrogen deficiency reduced leaf initiation and leaf enlargement but only leaf initiation recovered quickly when nitrogen was returned. This suggests that cell division within the developing leaf was reduced in the nitrogen-starved plants in agreement with the observations of Morton and Watson (6). It also suggests that cell division in the apex, which accounts for the initiation of new leaf primordia, was renewed while cell division within the expanding leaf was not renewed.

The physiological bases for the continued suppression of leaf enlargement and storage root growth after nitrogen return are not apparent. Particularly puzzling is the large effect that a 3-week interruption in nitrogen nutrition had on subsequent growth. It may be that nitrogen deficiency has such a general debilitating effect at all levels of metabolism and organization that considerable time is required for recovery. Our speculations have also included two, more specific, possibilities.

1. Nitrogen was resupplied as nitrate and reduction to the ammonium level must precede its utilization. Limitations in nitrate reductase activity (the enzyme is adaptive: 8) or in distribution of the assimilated nitrogen might effectively extend the period of nitrogen starvation in some plant tissues even in the presence of abundant nitrate. If this were the case, different recovery responses would be obtained if nitrogen were resupplied in a reduced form.
2. There is also a possibility that nitrogen deficiency caused injury to meristematic tissues in the root, and that some or all of the active supernumerary cambia failed to recover or were slow to resume activity when nitrogen was resupplied. The plate meristems in the expanding leaves appear to have behaved similarly while the terminal meristem recovered rapidly.

The results of the present experiment may also serve as basis for predicting optimum nitrogen-management practices for commercial production. With abrupt removal of nitrogen from the rooting medium, the transition from luxury level to deficient level of nitrogen nutrition required about 3 weeks. Maximum sucrose concentration, i.e., maximum quality, was attained after an additional 3 to 6 weeks with sucrose yields equal or higher than obtained with high nitrogen. As in earlier experiments (4, 5), these results indicate that field-grown sugar beet plants should be permitted to become nitrogen deficient at least 6 weeks prior to harvest. In fact, a longer period may be desirable for plants grown in soil where roots are able to continue growing into undepleted media and where nitrogen continually becomes available through nitrification processes.

Since plants which were returned to high nitrogen after 6 or 9 weeks of deficiency yielded less sucrose than either the continuous-high or continuous-minus nitrogen treatments, a further conclusion of practical significance appears warranted; viz., if nitrogen deficiency occurs within 3 months of harvest it would be better to continue the deficiency than to apply additional nitrogen. A similar response would be obtained if the resupply occurred naturally, e.g., if nitrogen, which had accumulated in the surface soil as a result of furrow irrigations during a dry season, was moved downward into the root zone by late season rains.

Summary

The responses of sugar beet to high- and minus-nitrogen nutrition, and during recovery from the deficient condition, were studied using nutrient cultures. Particular attention was given to growth of storage roots and of individual leaves, and to changes in sucrose content of storage roots.

At high nitrogen, new leaves were initiated at a relatively constant rate which was influenced little by other environmental factors. Leaf area per plant reached a maximum by mid-September and then declined due to a progressively smaller size of the new leaves. Nitrogen deficiency reduced root growth, rate of leaf initiation, leaf area, and dry matter accumulation, and increased sucrose concentration in the root. The degree of these responses was dependent upon the length of the nitrogen-deficiency period with sucrose concentration reaching a maximum after 9 weeks. The increase in sucrose was sufficient to compensate for the smaller size of roots so that equal amounts of sucrose were obtained from high- and minus-nitrogen plants during the first 9 weeks of the deficiency.

When nitrogen was returned after a brief deficiency, leaf initiation was renewed and the amount of sucrose accumulated in the roots declined. However, root growth and leaf expansion continued to be limited during the period of recovery at high nitrogen. Lower sucrose yields were obtained by returning nitrogen to the deficient plants than by allowing the deficiency to continue.

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